PELAGIC DISSOCONCHS OF THE COMMON MUSSEL, *MYTILUS EDULIS*, WITH OBSERVATIONS ON THE BEHAVIOR OF THE LARVÆ OF ALLIED GENERA.[1]

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The larvæ of the common black mussel, *Mytilus edulis*, are abundant in plankton samples taken throughout most of the summer in all regions where this mollusc occurs, Stafford, '12. Recognition of the larva, as Stafford points out, is rendered easy owing to its horn yellow color, its relatively small umbones and its small depth. To these characteristics may be added the distinctive shape of the shell, being more pointed and of shorter height at the anterior end, Fig. 1. The size of the mature prodissoconch when ready to attach varies considerably as judged from measurements of the largest larvæ obtained from the plankton, and from measurements of the prodissoconch shell of newly attached dissoconchs. Measurements of ten of the largest larvæ found in the plankton in Maine waters are as follows, antero-posterior axis being given first.

360 × 338 μ,	368 × 320 μ,
360 × 320 μ,	336 × 304 μ,
376 × 344 μ,	360 × 312 μ,
350 × 312 μ,	360 × 320 μ, exclusive of dissoconch rim,
336 × 304 μ,	304 × 280 μ, exclusive of dissoconch rim.

The last two larvæ, although caught in the plankton, each bore a narrow rim of purple dissoconch shell, Jackson, '88. From these and from other measurements made upon *Mytilus* larvæ it appears that dissoconch shell may be secreted at any time after the larvæ attain a length between approximately 300 and 360 μ. Stafford, *l.c.*, gives the measurements of two mature prodissoconchs as 345 × 310 μ and 400 × 331 μ.

[1] From the Zoölogical Laboratory of Rutgers University. Paper No. 14, New Jersey Oyster Investigation Laboratory.

The observations here reported were made during August, 1924 and August, 1927, in Frenchman Bay, Mt. Desert Island, Maine.[1] A collecting station some 100 meters from the labora-

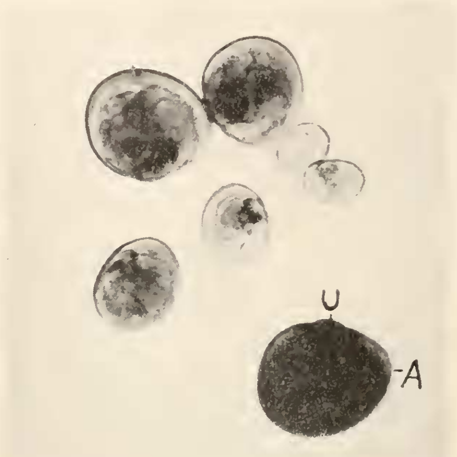


FIG. 1. Stages in the development of the prodissoconch larva of *Mytilus edulis*: *U*, umbones; *A*, anterior end.

tory point was marked with a buoy. With approximately 12 meters depth at mean low water this station lay in the full sweep of the tide through Frenchman Bay. Plankton samples of 25 liters were pumped here from various depths using a hose and oscillating clock pump, the majority of the samples being taken at the surface and at 7 meters depth. The *Mytilus* larvæ were collected by passing the water through a No. 18 treble extra heavy bolting cloth net, adding two or three drops of formalin to the catch and then drawing off the supernatant water bearing great quantities of the diatoms *Chætoceros* and *Rhizosolenia*. Table I. gives the numbers and stages of development of the mussel larvæ taken at the station, together with other data.

[1] It is a pleasure to acknowledge my indebtedness to the former Director, Professor Ulric Dahlgren, for the facilities given me at the Mount Desert Island Marine Biological Laboratory at Salisbury Cove, and for making early summer plankton catches for me.

TABLE I.

WATER CONDITIONS AND NUMBERS OF *Mytilus* LARVÆ AT STATION OFF LABORATORY POINT, FRENCHMAN BAY, MT. DESERT ISLAND IN 1924.

Date.	Time.	Tide.	Depth.	Temperature ° C.	Mytilus Larvæ in 25 Liters.	
					Prodissoconch.	Dissoconch.
Aug. 1.	—	—	Towing	—	—	1
5.	11:30 A.M.	2/3 flood	2 m.	10.6	Many	1
7.	3:00 P.M.	High	7 m.	11.0	262	
			0	13.3	753	
8.	3:45 P.M.	High	7 m.	10.9	336	
			0	17.1	71	
9.	11:30 A.M.	Low	7 m.	11.9	278	2
			0	15.6	5	
11.	10:15 A.M.	1/2 ebb	7 m.	13.7	63	
			0	14.3	6	
11.	10:30 A.M.	1/2 ebb	Towing	14.3	Many	8
12.	10:10 A.M.	1/3 ebb	7 m.	11.1	1,500	
			0	13.9	4	
13.	11:00 A.M.	1/6 ebb	7 m.	11.7	650	
			0	13.8	6	
13.	2:50 P.M.	3/4 ebb	7 m.	11.7	213	
			0	15.3	20	
14.	3:30 P.M.	1/6 flood	7 m.	12.3	240	1
			0	12.9	320	
15.	10:45 A.M.	High	7 m.	11.0	390	7
			0	12.9	1	
16.	11:20 A.M.	5/6 flood	7 m.	11.0	1	2
			0	12.9	177	
18.	10:50 A.M.	2/3 flood	7 m.	10.8	65	
			0	15.9	1	
19.	3:10 P.M.	High	7 m.	12.2	152	
			0	13.2	2	
20.	11:30 A.M.	1/3 flood	7 m.	11.9	56	
			0	12.7	2	
21.	2:50 P.M.	5/6 flood	7 m.	11.6	30	
			0	12.0	4	
22.	5:00 P.M.	High	7 m.	11.4	24	1
			0	14.7	5	
23.	3:10 P.M.	2/3 flood	7 m.	11.0	17	
			0	13.7	7	
25.	3:00 P.M.	1/3 flood	7 m.	11.7	40	1
			0	13.1	10	
27.	3:45 P.M.	1/6 flood	7 m.	12.3	19	
			0	13.9	7	

PELAGIC DISSOCONCHS OF *Mytilus*.

(*a*) *Buoyancy through Gas Secretion.*

In the tow sample taken by Professor Dahlgren August 1 was found one *Mytilus* larvæ which bore the distinct rim of purple shell which marks the commencement of the dissoconch stage.

Since only one such mussel was found it was believed to have been accidentally introduced through the townet striking some object bearing attached mussels. Subsequent collections, however, revealed numerous dissoconchs up to 941 μ in length freely floating about at various depths up to 7 meters. A 25 liter sample pumped August 13, from the surface, 20 cm. from a *Mytilus*-covered pile, yielded 200 *Mytilus* larvæ from mature prodis-

FIG. 2. Pelagic dissoconch of *Mytilus edulis* approximately .8 mm. in length, bearing a large bubble of secreted gas within the branchial chamber. This specimen came from a depth of 7 meters.

soconchs to advanced dissoconchs over 900 μ in length. A similar sample pumped August 15 from a depth of 7 meters at the collecting station, more than 100 meters from the nearest mussel beds, gave 390 prodissoconch *Mytilus* and 7 dissoconchs which ranged in length from 445 to 784 μ.

The presence of well-developed dissoconchs floating freely in the water at once raises the question of the means by which this is effected in the absence of the swimming organ or velum of the prodissoconch. When brought to the laboratory for examination these dissoconchs were found to be identical with others removed from sea weeds, save for the presence of a large clear space in the posterior portion of the pallial cavity. Believing that some change might have occurred in the molluscs even during the fifteen minutes to half an hour which elapsed between their capture and subsequent examination in the laboratory, a binoular was taken in the boat and the young mussels were examined immediately after their capture. The result is shown in Fig. 2. A large bubble was found to occupy the posterior part of the pallial cavity, its buoyancy causing the young bivalve to hang suspended in the water umbone downward, with the postero-ventral margin of the valves turned upward. On one occasion the bubble was seen to form through the coalescing of many minute bubbles, which, passing slowly down between the gill filaments, united to form a single large bubble. In several individuals two or three smaller bubbles were found. Where a single bubble was present its size was such as to cause a thinning of the mantle on either side and a forward displacement of the posterior gill filaments, thus accounting for the large clear space already noted in the posterior pallial cavity of the young *Mytilus* dissoconchs first taken.

Failure to observe the bubble in larvæ first brought to the laboratory was due to the fact that as soon as a *Mytilus* dissoconch comes in contact with any object the foot is rapidly extruded from between the valves and brought into contact with the surface. The extrusion of the foot, accompanied as it is by a separation of the valves and of the applied lobes of the mantle, results in the immediate escape of the bubble in nearly every instance.

The composition of the gas in the bubble was not determined owing to its small size and lack of adequate facilities for a micro-chemical test. The fact that it forms within the gills would indicate that it is mainly oxygen. The composition of gas secreted into the swim bladders of fishes renders this still more probable.

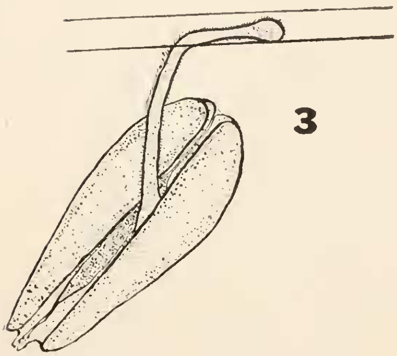
The possibility that the bubbles within the branchial chamber of these young *Mytilus* might have been air introduced accidentally during passage through the pump or while in the net, was tested in the following manner. The hose was disconnected from the pump and allowed to siphon water from a depth of 7 meters into the net held in the bottom of the boat. The stream entered the net under water and great care was taken not to agitate the net or to break the water surface. Dissoconchs of *Mytilus* collected in this way revealed the same large bubbles as before. Dissoconchs of *Mytilus* collected from sea weeds and violently shaken with a little sea water in a bottle failed to acquire any bubbles of air in the process; thus, with the above experiment, proving that the bubbles of gas were not accidentally introduced.

To determine the possible effects of pressure in bringing about gas secretion pieces of glass tubing 2 cm. long were cut and an early *Mytilus* dissoconch obtained from sea weeds was introduced into each. A piece of coarse bolting cloth was tied over each end of the tubes which were then fastened to a line at one meter intervals and suspended from a float at the collecting station. One string bore seven tubes which hung at depths of from two to eight meters. A second string was attached to a weight on the bottom with a float of sufficient size to hold the string vertically in the water, the lowest tube being at 11 meters depth at low water and approximately 15–16 meters at high water. When removed 48 hours later all of the bivalves were found to have attached by the byssus to the inside of the tubes or to the bolting cloth ends. When removed to a dish of sea water they crawled actively about with the foot. In no case was a bubble present. Either the stimulus to gas secretion is absent when the mussels are attached, or the frequent extrusion of the foot which occurs while the mussel is attached permits the escape of such gas as rapidly as it is formed.

(*b*) *Attachment to the Surface Film.*

If the surface of the water near a mussel bed or near a mussel covered piling be skimmed with a plankton net during the latter part of the breeding season, numerous dissoconchs will be found. They are most numerous as the rising tide first sweeps over the mussels and attached sea weeds. A microscopic examination of these dissoconchs shows that none contains a bubble, hence it is obvious that these young mussels must maintain themselves at the surface through means other than the gas secretion employed by larvæ at a depth. When placed in a dish of sea water such larval mussels exhibit great activity, gliding about upon the long, highly adhesive, ciliated foot as rapidly as a snail. Observations were made upon these young molluscs using a chamber 0.5 cm. wide made of two microscopic slides, filled with sea water and viewed horizontally through the binocular.

Once in contact with a solid object, such as the wall of the chamber, a rock, or a fragment of sea weed, the mussels exhibited a marked negative geotropism and climbed straight upward until the surface was reached. Here the distal one third to one tenth of the foot was extended in the surface film, Fig. 3, and with a quick contraction of the foot, aided apparently by contraction also of the pedal retractor muscles, the ventral margins of



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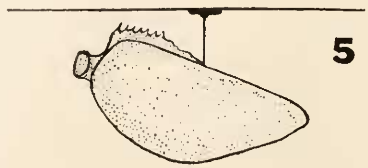

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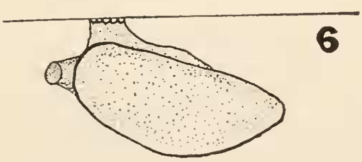

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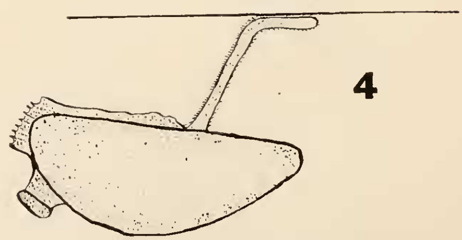

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Fig. 3. Ventral view of *Mytilus* dissoconch, 4 mm. long, hanging from the foot in the surface film, as seen from the side and partly from above.

Fig. 4. Lateral view of 4 mm. *Mytilus* dissoconch hanging from the surface film. The siphons are fully extended.

Fig. 5. Lateral view of 3 mm. *Mytilus* dissoconch hanging from byssus thread attached to holdfast secreted in the surface film. The foot, which was fully extended in the surface film while secretion of the holdfast was effected, has been wholly withdrawn between the valves.

Fig. 6. Lateral view of 3 mm. *Mytilus* dissoconch holding to the surface film with the aid of the tentacles of the incurrent siphon. The foot which serves to hold the mussel close to the film until the siphon is inserted therein, has been withdrawn between the valves.

the mantle were brought into contact with the surface film. While lying with the entire ventral margin of the body in contact with the surface film the byssus gland in a few seconds secreted onto the surface film a small holdfast similar in appearance to that which is laid down on rock or piling for the attachment of each byssus thread. A thread 1–2 mm. long serves to support the young mussel from this float and with foot withdrawn it may hang suspended indefinitely, Fig. 5. At times it thrashes about with the foot fully extended as though in search of some solid surface for attachment. When the foot strikes such an object the mussel glides quickly upon it, trailing the byssus thread behind or breaking it off. The "float" is not a buoyant structure, since when pushed beneath the surface film it rapidly sinks. It maintains its position in the surface film, supporting mussels up to 4 mm. in length, solely through surface tension.

A float and connecting thread are not always secreted when the young mussel reaches the surface. At times it supports itself solely by the distal end of the foot in the surface film, Fig. 4, after the manner described for the prodissoconch oyster larva, Nelson, '24a. With the aid of the numerous short cilia covering the foot the animal glides slowly along the surface film, rocking the body slowly from side to side and occasionally through a quick contraction of the proximal portion of the foot, bringing the entire ventral margin of the shell in contact with the surface film. This behavior will recall the familiar habit of pond snails of hanging from the entire foot spread out in the surface film.

A third mode of suspension from the surface consists in extending the tips of the tentacles of the incurrent siphon into the film and hanging from these, Fig. 6. This behavior, though seldom observed, serves to support the mussel quite as effectively as does the foot.

Such floating dissoconchs have never been found further than approximately 25 meters distance from mussel beds or mussel covered piling. Their abundance, 5 to 100 per 25 liters of water, close to such habitats indicates that young mussels frequently make use of this mode of transportation for covering short distances.

Examination with the low power binocular of several small tide pools close to the laboratory revealed numbers of *Mytilus* 3–4 mm. long moving actively over the rocks and barnacles while others were at the surface. With the incoming tide the latter are carried away and may eventually reach a place of attachment at a considerable distance.

Metamorphosis in Allied Lamellibranchs.

The water samples taken in Frenchman Bay contained in addition to the larvæ of *Mytilus edulis,* great numbers of the young of the soft clam, *Mya arenaria,* together with occasional specimens of the larvæ of *Venericardium,* of *Anomia* and possibly also of *Astarte.* During more than ten years study of the oyster larvæ of the New Jersey Coast I have become familiar also with the larvæ of *Mytilus recurvus* (the southern oyster mussel), *Venus mercenaria,* and *Teredo navalis.* In no instance have I ever observed gas secretion in any of these forms nor have I found pelagic dissoconchs. When the time for setting arrives the mature larvæ of all of the above species disappear from the water within 24 to 36 hours.

Reproduction and dispersal of marine pelecypod molluscs occur through the medium of pelagic veligers which are free-swimming for periods ranging from a few days in such incubatory forms as *Ostrea edulis* and *Teredo bartschi,* to approximately three weeks in *Mytilus edulis, Mya arenaria,* and in probably most of the marine bivalve molluscs which reproduce at temperatures below 20° C., Nelson, '28. Owing to the sessile or sedentary habits of the adult molluscs, the activities of the larvæ become of first importance in the dissemination and preservation of the species. Through the aid of the velum the larval bivalve, while unable to make progress against a current, can control its vertical distribution and thus secondarily may determine to a marked degree its horizontal distribution by tides and currents, Nelson, '22.

The rate of growth and of development during larval life is determined chiefly by the temperature. The long series of observations on the life history of the American oyster, *Ostrea virginica* Gmelin (J. Nelson, Stafford, Churchill, T. Nelson and others), indicates that at a given temperature the duration of the pelagic period is remarkably constant. With an average temperature of 23–24° C. the period from spawning to the attachment of the spat in New Jersey waters is 13 days. In Richmond Bay, Canada, J. Nelson, '17, found that at temperatures approximating 20° C. the minimum time required for oyster larvæ to mature was 17 days. Stafford, '13, considers three weeks to be the average time required to reach maturity in Canadian waters.

The close of the free-swimming period of pelecypod larvæ is determined apparently by internal developmental factors: when the time for "setting" arrives the larvæ must attach or die. Since the veligers during their pelagic existence have been distributed widely by currents it follows that for those which through chance happen to "fall upon good ground" there will be many more which through this same chance will "fall by the wayside" and be destroyed.

Observations of the oyster larva, T. Nelson, '22, '24, show that approximately 24 hours prior to attachment the young bivalve becomes positively stereotropic and that it may explore numerous surfaces with the aid of the foot before it finally attaches. Such behavior, while of the utmost importance in securing a favorable spot for attachment, is without avail if no substrata suitable for attachment are present. Little is known of the factors necessary to provide a favorable bedding ground for such burrowing species as *Mya* and *Venus*. Although attachment of young *Mya* by the byssus to sea weeds or other objects may occur, as shown by Ryder, '89, and by Kellogg, '99, it is pointed out by Belding, '12, that survival of both *Mya* and *Venus* depends largely upon the character of the mud and sand forming the surface layers of the bottom. All who have studied the habits of larval bivalves agree that the vicissitudes of larval life and subsequent attachment form one of the chief barriers to wide dispersal of the species.[1]

[1] A survey of our present knowledge of the habits and life histories of both fresh-water and marine pelecypods shows that of all environmental influences the presence of a suitable substratum is the most important single factor limiting distribution. The following papers may be cited in this connection: fresh water mussels, Coker et al., '21; *Mya*, Belding, '09; *Pecten*, Belding, '10; *Venus*, Belding, '12; *Ostrea cucullata*, *O. angasi*, Roughley, '25; *Mytilus*, *Cardium*, *Saxidomus*, *Siliqua*, *Paphia*, and other genera of the Pacific Coast, Thompson, '13, and Weymouth, '20; *Ostrea*

Of the known genera of marine pelecypods, *Mytilus edulis* and *Teredo navalis* alone are circumpolar in their distribution over the shores of the northern hemisphere. General adaptability to changing conditions and the power to resist adverse surroundings together with relatively low spawning temperatures, Nelson, '28, have aided these two forms in attaining their present wide distribution. Transportation through attachment to vessels or to other floating wood has likewise aided in their dispersal, being for *Teredo* the only means by which any great distance could be covered. In the case of *Mytilus edulis,* however, the ability to bridge the period of metamorphosis while remaining pelagic must have been an important factor in securing the wide dispersal which this mollusc now enjoys; as well as a great aid in bringing to a suitable place of attachment a fair proportion of the larvæ produced each season. The largest of the pelagic dissoconchs found in Frenchman Bay was fully a month old, during which time it must have been transported over long distances by the tide. If during this period it had come in contact at any time with a solid object attachment could easily have been effected.

Summary.

At the close of the larval or prodissoconch stage the young of *Mytilus edulis* which fail to secure immediate attachment may remain pelagic through the secretion of gas into the mantle chamber.

Short distances may be covered through the aid of a holdfast secreted on the surface film or through holding the foot or the tentacles of the incurrent siphon in the surface film.

The ability to bridge over the critical period of metamorphosis while remaining pelagic has been an important factor in securing the present wide distribution of the black mussel.

Absence of a similar adaptation in the larvæ of other bivalves renders them still dependent largely upon chance in securing at the close of the pelagic period a proper substratum for attachment. This dependence upon the substratum is one of the chief barriers to the wide dispersal of the species.

virginica, Moore, '97, Grave, '01, Stafford, '13, J. Nelson, '17, Churchill, '20, T. C. Nelson, '22.

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